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ALTITUDINAL VARIATION IN NEW GUINEA BIRDS

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INTRODUCTION

The study of the bird collection of the American Museum's 1933–1934 Papuan Expedition, sponsored and led by Richard Archbold has brought out the hitherto unrecognized fact that in New Guinea there is considerable geographical variation in certain species of birds which is correlated with altitude.

Altitudinal variation, in which the forms from the higher altitudes are larger and darker, due to the colder and more humid (cloud belt condition) environment, are well known from tropical mountains.

The only undoubted altitudinal races that had been recognized as such in New Guinea were described by Ogilvie-Grant. These are *Collocalia hirundinacea excelsa*, a mountain representative of *C. h. hirundinacea*, and *C. esculenta erwini* (described as *maxima*), a mountain representative of *C. e. esculenta* (1914, Bull. Brit. Ornith. Club, XXXV, pp. 34, 35). Such well-known cases as *Syma megarhyncha* and *S. torotoro*, *Peltops montanus* and *P. blainvillii* are properly species which represent each other at different altitudes.

AIM AND SCOPE OF THE WORK

New Guinea is a very mountainous island, with peaks rising to 5000 meters, and it would have been surprising if cases of altitudinal variation and altitudinal representative races did not exist. In the present paper I shall show that altitudinal variation does exist in New Guinea and that in many cases it is in accordance with the rules which appear to govern the same phenomenon in other parts of the world.

The present work is based largely on the bird collection made by the 1933–1934 Papuan Expedition (Richard Archbold and A. L. Rand). A collection made by the The Whitney South Sea Expedition (Mr. Hannibal Hamlin) in southeast New Guinea and a collection made by Mr. J. T. Zimmer in southeast New Guinea were useful in supplying lower altitude specimens. A complete report on these collections by

Dr. E. Mayr and myself is being prepared, and the intention of the present paper is to draw attention to the heretofore overlooked fact that altitudinal variation commonly occurs in New Guinea. My thanks are due to Dr. Mayr for criticisms in preparing this paper.

The present survey covers only part of southeast New Guinea and, in the subsequent discussions, the altitudes used refer to the following areas.

Sea level: chiefly the lowlands near Yule Island, but in a few cases specimens are included which come from between the St. Joseph River and Milne Bay.

770 meters: Deva Deva, Iola and Fane (these localities were collected chiefly by Mr. Hamlin with the aid of natives so that a rather large vertical range was probably covered).

1250 " Mafulu
1400 " Bella Vista and Fane
1800 " Ononge
2000 " Mt. Tafa, east slope
2400 " Mt. Tafa, west slope
2800 " Murray Pass
3600 " Mt. Albert Edward

Thus, the area discussed is roughly a cross-section of southeast New Guinea from Yule Island to the top of the Wharton Range at Mt. Albert Edward. For a map and description of this area, see 'Results of the Archbold Expeditions, No. 7,' 1935, Bull. Amer. Mus. Nat. Hist., LXVIII, Art. 8.

ALTITUDINAL RACES

Examples

A number of altitudinal races have been described in an earlier report by Mayr and Rand ('Results of the Archbold Expeditions, No. 6,' 1935, American Museum Novitates, No. 814), and these, with other races that have been described, are discussed below.

Grassland Forms

Synoicus ypsilophorus mafulu Mayr and Rand, from the mountain-valley grasslands between 1000 to 2000 meters. This race is slightly larger, more barred and with less sexual dimorphism than the lowland *plumbeus*.

Synoicus ypsilophorus monticola Mayr and Rand, from the alpine grasslands above 2800 meters. This race is distinguished from both *mafulu* and *plumbeus* in being larger, more coarsely barred, lighter in general color and in having the sexual dimorphism still more reduced.

These two forms are especially interesting in that of all the other races of *ypsilophorus*, *mafulu* is most like *australis* of eastern Australia, while *monticola* is most similar to *ypsilophorus* of Tasmania.

Megalurus timoriensis alpinus Mayr and Rand, from the alpine grassland above 2800 meters. This race differs from the lowland form *macrurus* in its larger size, heavier markings, grayer flanks and darker rump.

Megalurus timoriensis macrurus from 1000 to 2000 meters is not identical with the lowland bird (see below).

Malurus alboscapulatus mafulu Mayr and Rand, from the mid-mountain grasslands between 1000 and 2000 meters; this differs from the lowland *naimii* in its larger size and the greater extent of black in the female. This species is broken up into a number of races in New Guinea in which the range of a black-bellied form sometimes separates the range of two white-bellied races, so that the ranges of two very similar white-bellied, forms such as *tappenbeckii* and *alboscapulatus*, are separated by the range of the more different *aida* with a black belly.

Lonchura caniceps scratchleyana Sharpe was described in 1889 (Bull. Brit. Ornith. Club, VII, p. 9) but has apparently often been overlooked. From the description it might be confused with *L. c. kumusii* Hartert, but is quite a different looking bird; *kumusii* is simply a paler, grayish-brown race of *caniceps*, while *scratchleyana* is more different. It is paler, more earthy brown and with paler upper tail-coverts than *caniceps* and much more earthy brown than *kumusii*. In size, *scratchleyana* does not differ from *caniceps*.

Forms of Both Forest and Grassland

An example of this is *Collocalia esculenta*. The following measurements are given from the material from southeast New Guinea.

	Meters	Male	Female
erwini	3600	109, 110, 110 mm.	108
esculenta	2800	104, 106	
	2400	104, 104, 105, 106, 107	103, 104, 107
	2000	102, 102, 103	103
	900		109
	450	103	101, 101

This is a bird which lives in the forest as well as about the forest edges and feeds over the edge of the grassland.

A differentiation in both size and color correlated with altitude is suggested in *Collocalia hirundinacea*, but the present material is not

sufficient to be sure of this. Ogilvie-Grant (1914, Bull. Brit. Ornith. Club, XXXV, p. 34) found that in the Snow Mountains the birds from the higher altitudes were different enough from *hirundinacea* of the lowlands to justify separating it as *excelsa*.

Forest Forms

Our work on the Wharton Range has also established the fact that there are altitudinal races of three forest birds.

Ptiloprora guisei perstriata DeVis has usually been synonymized with *guisei*, but actually the name refers to the larger, dark-backed, not rufous-backed, form from the highest altitudes on the Wharton Range where we collected it at 3680 meters. *P. guisei*, with the feathers of the back edged rufous, ranges from 2000 to 2800 meters. In this connection it should be stated here that *perstriata* is very similar to *lorentzi* from the Snow Mountains, and *praedicta* of the Wandammen Mountains, while *guisei* is more similar to the rufous-backed form *umbrosa* of the Sepik Mountain; *mayri* of the Cyclops is somewhat intermediate between the black and rufous-backed forms. This similarity of *perstriata* to *lorentzi* and the greater difference from *guisei* suggests a different history for the higher race, and possibly it has not evolved from the lower ranging *guisei*.

The name *Melidectes leucostephes belfordi* DeVis has usually been considered as applicable to all the southeast New Guinea birds, but from the collections of the 1933–1934 Papuan Expedition it appears to be applicable only to the form from the highest parts of the Wharton Range, which we collected only at 3680 meters on Mt. Albert Edward; this form differs from the lower altitude race (*M. l. brassi* Mayr and Rand) which we found from (1400?) 2000 to 2800 meters, only in its larger size.

	Meters	Male	Female
belfordi	3680	147, 150, 150, 153, 153 mm.	140
brassi	2800	139	127, 131
	2400		139
	2000	140, 141, 143, 143, 144	127, 130, 131
	1400 (?)	132, 140, 148, 144	123, 127, 137

Judging by the similarity between *brassi* and *belfordi*, and the greater difference from other races of *leucostephes* (a contrast to the condition in *Ptiloprora*) there seems little doubt that one is the ancestor of the other.

Sericornis nouhuysi monticola Mayr and Rand, from 3680 meters on Mt. Albert Edward, is distinguished from *oorti* occurring on Mt.

Tafa by its average slightly larger size and its considerably paler, less brown coloration.

Summary of All the Altitudinal Races

Higher altitudinal races which are larger than their lowland representatives:

**Synoicus ypsilophorus mafulu*
**Synoicus ypsilophorus monticola*
**Megalurus timoriensis alpinus*
**Malurus alboscapulatus mafulu*
Collocalia esculenta erwini
**Sericornis nouhuysi monticola*
**Ptiloprora guisei perstriata*
Melidectes leucostephes belfordi

Higher altitudinal races which are darker than their lowland representatives:

Synoicus ypsilophorus mafulu
Megalurus timoriensis alpinus
Malurus alboscapulatus mafulu
Ptiloprora guisei perstriata

Highland races which are paler than their lower altitudinal representatives:

Lonchura caniceps scratchleyana
Synoicus ypsilophorus monticola
Sericornis nouhuysi monticola

Analysis of the Above Data

Of these nine higher altitudinal representatives eight or 88.8 per cent are larger than their representatives from the lower altitudes; four or 44.4 per cent are darker than their lower representatives; three or 33.3 per cent are paler than their lower races; two or 22.2 per cent do not differ in color.

ALTITUDINAL VARIATIONS WHICH ARE NOT OF SUBSPECIFIC VALUE

Besides these cases in which the difference between populations from different altitudes is great enough to justify separating them as races, there are a considerable number of cases in which there is a difference correlated with altitude, but it is too slight to be used in recognizing races, or there is too much overlap or intergradation over too great an area.

* Differ also in color.

A vertical range of 800 meters is the smallest within which I have found a recognizable variation, so that in the following discussion only forms are included in which we have sufficient material separated by at least 800 meters of altitude. At least two specimens from one extreme and four from the other with regard to comparable age and sex, immature birds being discarded, are considered as sufficient to give an indication of the variation or lack of it, and in most of the cases where variation was found considerably larger series are at hand, as can be seen from the accompanying data. In a few cases where more than the minimum material was present a slight difference in size was indicated, but it did not seem definite enough to list; these cases are excluded from the following tabulations.

Examples

The following are examples of variations which are not great enough to use in separating races.

Variations in Size (Wing Length)

Paramythia montium

Meters	Male	Female
3680	97, 99, 101, 103, 107 mm.	101, 102, 102, 102
2800	101, 103, 106	94, 100, 100, 102
2400	95, 98, 101, 104, 104	93, 95, 96, 97
2300	103	91

In this case, over a range of 1300 meters, the only difference is one of size, and that is clearly shown only in the female. *Acanthiza murina*, ranging from 2400 to 3680 meters, shows a similar size difference, most noticeable in the female though also evident in the male, as does *Rhipidura brachyrhyncha* and *Ifrita kowaldi*.

In some cases the difference is noticeable in both the male and the female, as in *Pachycephala schlegelii* with a range from 770 to 3680 meters.

Meters	Male	Female
3680	91, 91, 92, 93, 94 mm.	87
2840	86, 89, 90, 90, 92, 92, 94	87, 88, 89
2400	87	88
2070	86, 86, 87, 88	83, 85, 86, 86
1250	86	
770		83, 86

A similar condition was found to exist in *P. schlegelii* in the Saruwaged Mountains, by tabulating Mayr's data in 1931, Mitt. Zool. Mus. Berlin, XVII, p. 672.

Crateroscelis robusta also shows the same thing.

Meters	Male	Female
3680		60. 63
2860	64, 65, 66, 66 mm.	60, 61, 62, 63
2400	61, 62, 62, 62	59, 60, 60
2000	61, 61, 62, 62, 63, 64	57

In these cases the difference is one of size only.

Similar well-marked cases are *Machaerirhynchus nigripectus*, *Pachycephala rufinucha* and *Peltops montanus*.

In some cases the difference in size is more pronounced in the male, as the following data on *Poecilodryas sigillata* show.

Meters	Male	Female
3680	100, 100 mm.	93, 94, 96
2840	96, 99	90
2400	92, 92, 93, 93	89, 90, 92, 92

The following are extremes of this type of variation in non-passerine birds:

Aegotheles insignis

Meters	Male	Female
2400	176 mm.	176
1800	171	
1250	162, 170	172, 172

Macropygia amboinensis[1]

Meters	Male	Female
1250	171, 174, 174 mm.	168
450	172	
Near sea level	168, 170	161, 167

Rallicula forbesi

Meters	Male	Female
2800	107, 113, 115, 116, 117, 117 mm.	112, 114, 116
2400	107, 115, 117, 117	
1250	105, 111	
770(?)		108, 109

[1] Mayr, 1931, Mitt. Zool. Mus. Berlin, XVII, p. 707, says that north New Guinea birds of this species from the higher altitudes are darker than lowland specimens.

There are many other cases which suggest the same increase in size with altitude, but the data at hand on these species are too scanty to use in generalizing. This is particularly true of the non-passerine species, in which large series were as a rule not collected.

There is, however, one case (the following) in which the birds from a higher altitude are smaller than those from lower altitudes.

Pitohui dichrous monticola

Meters	Male	Female
1250	106, 108, 109 mm.	106, 106, 107
Near sea level	111, 111	109, 109

This is the only such case that I have seen in the New Guinea collection.

Variations in Color

The above variations deal only with size. There are also a number of examples of color variation with altitude but no difference in size, of which the following are examples.

Myiolestes megarhynchus despectus. Some of the specimens from 1250 meters are much darker, more earthy colored below than the series from sea level while other specimens are identical. There is no average difference in size.

Specimens of *Megalurus timoriensis macrurus* from the 1000–2000 meters mountain grassland are slightly darker and more heavily marked than the lowland birds.

Pachycephala griseiceps perneglecta. In this species the birds from 1250 meters have a grayer, less brownish (that is, lighter colored) crown than birds from near sea level.

Summary

A Summary of the Species Which Show Altitudinal Variation within a Subspecies and Those Showing No Variation

In the following lists I have not chosen material from any group or groups of birds, but have included all the species on which I have sufficient data (see above, p. 6, for criterion used in selecting data). Naturally smaller series of the larger species were collected, and though altitudinal variation was indicated in some, it is due to insufficient data that these are not included. Young birds were not used in making comparisons, and due to differences in sex other series were not usable so that in all there are left only sixty species to be used in the following tabulation.

Forms in which representatives from the higher altitudes are larger:

Rallicula forbesi	(770?)	1250–2800 m.
Macropygia amboinensis		6–1250
Aegotheles insignis		1250–2400
Collocalia esculenta esculenta		450–2800
Collocalia vanikorensis		0–1250
Crateroscelis robusta		2000–3600
Ifrita kowaldi		2000–3600
Acanthiza murina		2400–3680
Poecilodryas sigillata		2400–3680
Rhipidura brachyrhyncha		2000–3600
Machaerirhynchus nigripectus		1250–2400
Peltops montanus		770–2000
Pachycephala schlegeli		2000–3680
Pachycephala rufinucha		770–3680
Paramythia montium		2300–3680

Species in which the higher altitudinal representative is smaller:

Pitohui dichrous	0–1250 m.

Species in which the higher altitudinal representatives are darker:

Megalurus timoriensis macrurus	0–2000 m.
Myiolestes megarhynchus	0–1250

Species in which the upper population is paler:

Pachycephala griseiceps

The series I have of the following forms do not show altitudinal variation:

Ieracidea berigora	100–2400 m.
Ptilinopus pulchellus	0–1250
Ptilinopus rivolii bellus	1250–2800
Ducula chalconota	770–2400
Gymnophaps albertisii	2000–3680
Macropygia nigrirostris	0–1450
Reinwardtoena reinwardtsi	0–1250
Lorius lory	0–1250
Trichoglossus ornatus	0–1450
Oreopsittacus arfaki	2400–3680
Neopsittacus muschenbroekii	1250–2800
Neopsittacus pullicauda	2400–3680
Psittacella picta	2400–3680
Cacomantis castaneiventris	100–1250
Cacomantis pyrrhophanus	2000–2800
Podargus papuensis	0–2000
Aegotheles albertisi	2000–2800
Edolisoma montanum	770–2000

Coracina longicauda	2000–2800
Turdus poliocephalus	2400–3680
Melampitta lugubris	2000–2800
Sericornis papuensis	2000–3680
Phylloscopus trivirgatus	1270–2400
Arses telescopthalmus	0–1250
Rhipidura albo-limbata	2000–3680
Rhipidura atra	1000–2400
Pachycephala modesta	2000–3680
Myzomela rosenbergi	1250–3680
Melipotes gymnops	1250–3680
Melidectes torquata	770–1500
Melidectes fuscus	2800–3700
Melidectes leucostephes brassi	2000–2800
Oreornis subfrenatus	2000–3680
Xanthotis chrysotis	0–1250
Ptiloprora guisei guisei	2000–2800
Dicaeum geelvinkianum	0–1800
Melanocharis nigra	0–1250
Pristorhamphus versterii	1250–3680
Oreocharis arfaki	1250(?)–2840
Zosterops novaeguineae	1250–2400
Lonchura monticola	2800–3600

Analysis of the Above Tabulation

In all, I have included sixty species of which I have material enough to judge whether or not there is variation correlated with altitude. Of these, nineteen species or 31.6 per cent show some variation; in 15 or 25 per cent of the total number of species examined there is an increase in size with altitude; in two cases or 3.3 per cent of the total the representatives from the higher altitudes are darker. In only one case, 1.6 per cent, are the higher altitude specimens smaller. In one case, 1.6 per cent, the higher altitude specimens are a paler color. Of the sixty species discussed, seventeen, or 28.3 per cent, show an increase in size or in pigmentation with increase in altitude, while in only two, or 3.3 per cent, of the cases is the reverse true.

The altitudinal variation is more common in the passerine birds:

	Showing Variation	Not Showing Variation
Non-passerine forms	5 (distributed in 4 families)	17 (in 7 families)
Passerine forms	14 (in 6 families)	24 (in 10 families)

Thus, of the twenty-two non-passerine forms, five, or 22.7 per cent, of them show altitudinal variation, and this is in size only; of the thirty-

eight passerine birds, fourteen, or 36.8 per cent, show altitudinal variation.

DISCUSSION

The races of grassland species have the ranges of the different populations at different altitudes quite separate; the grasslands and savannas of the lowlands, the mountain-valley grasslands, from 1000 to 2000 meters, and the alpine grasslands above 2800 meters are separated from each other by belts of forest. Since the ranges are not continuous, intergradation is possible only through individual variation.

That the isolation of these grasslands by forest barriers is the sole factor involved is unlikely when we consider that birds less restricted to grasslands also show size differences correlated with altitude.

The two honey eaters with altitudinal races are both forest birds with a continuous range in the continuous forest from 2000 to 3680 meters, and yet both range from 2000 meters on the mountain slopes to 2800 meters on top of the Wharton Range unchanged, without a progressive differentiation as the altitude increased, while the forms found on Mt. Albert Edward at 3680 meters (and probably on other isolated mountain peaks in southeast New Guinea which rise to sufficient height, as the types of *P. g. perstriata* and *M. l. belfordi*, come from Mt. Knutsford to the southeast of Mt. Albert Edward) are definitely different, suggesting a sudden change from one form to the other or a narrow area of intergradation.

Sericornis nouhuysi is also a forest bird with a continuous vertical range, but in this form 2800 meters is in the area of change between the two races. Most of the specimens from 2800 meters are definitely referable to *oorti*, some with a slight tendency toward *monticola*, while two of them are definitely *monticola*. This suggests that the area of intergradation between these two forms may be very narrow, if we consider that a 100 meter vertical range from the camp altitude was collected over, and the typical *monticola* may have come from the upper part of this range.

This is in contrast to the case of *Collocalia esculenta* (see above), in which there is a gradual increase in size until the extreme in size, from the highest altitude, may be recognized as a slightly differentiated mountain race.

In variations not great enough to be of subspecific value which show an increase in size with increase in altitude, sometimes more pronounced in one sex than the other, sometimes noticeable in both, there is, in the

cases on which I have data, a gradual change in size; that is, there is no sharp, sudden change from a population of one size to that of another size.

This appears to be different from the above mentioned cases of altitudinal races, where the change may be sudden, but is similar to the condition in *Collocalia esculenta* with a slightly differentiated mountain race.

In the above I have set forth a number of slight variations correlated with altitude and a number of altitudinally representative subspecies. These largely conform to the Bergmann rule. These should be the forerunners of species, and should give an idea of one manner in which mountain species may originate.

Dr. Chapman, in his most recent work on the distribution of birds in South America (1931, Bull. Amer. Mus., LXIII, pp. 40–41), states that the mountain forms on Roraima and Duida Mountains are usually larger and darker than their assumed ancestors, in conformation to the laws that species increase in size with higher altitudes, and become darker in color with greater humidity. He further holds that whatever the process which accomplishes this, it is apparently started by the influence of environment.

Bates (1931, Ibis, pp. 255–300) has pointed out that certain small variations correlated with altitude occur in the mountains of west Africa; but Chapin, in his study of the African montane avifauna (1932, Bull. Amer. Mus., LXV, pp. 285–300), finds few montane species which appear to have been derived from present lowland forms. Chapin is of the opinion that heredity and mutation, with the aid of isolation, determine how the bird will vary, and climate acts only as a selective factor.

In New Guinea the populations at different altitudes, which differ slightly from each other, are presumably the forms which have only recently begun to vary. They have not yet had time to evolve further. We should also expect to find in New Guinea, an island which has had time to develop a very peculiar montane fauna, a series of closely related altitudinally representative species. But it is impossible to find many of them. In the genera such as *Pachycephala*, *Poecilodryas*, *Myzomela*, *Rhipidura* and *Gerygone* with representatives from sea level to timber line, it is impossible to find lowland forms from which the montane species really appear to have been derived. There are a few exceptions such as occur in the genera *Peltops* and *Syma*, but there are also examples of species with altitudinally overlapping ranges which are just as similar (such as *Erythrura*, *Collocalia* and *Neopsittacus*) or very similar species

with the same vertical range (as in *Meliphaga*). The chains seem to be broken here. There is no series to show that the influence of altitude on climate has brought about the evolution of mountain species along certain lines. There are many very distinct mountain forms, but most of them are not closely enough related to existing lowland forms to be able to point out their ancestry.

SUMMARY

Altitudinal variation within a species is a common phenomenon in the mountains of southeast New Guinea. It occurs both in species inhabiting areas of grassland isolated at different altitudes by forest belts and in birds inhabiting the forest which is continuous from one altitude to another.

In nine cases these differences are great enough to use in recognizing races; in nineteen cases these differences are not great enough or there is too great an area of intergradation or overlap to characterize races. In forty-one species in which I have enough material to arrive at a conclusion, there is no altitudinal variation.

Increase in size, correlated with increased altitude and consequently lowered temperatures, is the most common type of variation (in eight races and fifteen cases of smaller variation); there was only one race which showed no size variation and one case in which the higher altitudinal population was smaller.

Variation of pigmentation was found in seven races and in only three cases within subspecies. Increased pigmentation is usually associated with increased humidity so that only the Subtropical Zone forms would be expected to be darker. This is true in *Sericornis nouhuysi*, with a paler Upper Temperate Zone race, but is not the case with *Ptiloprora guisei*, though here other factors may come in. With the other races there does not seem to be a definite general tendency toward lightness or darkness with increase in altitude. Possibly when the climatic conditions in the mountains of southeast New Guinea are known this may help to explain the variation in pigmentation.

Though I have few examples, the forest species which have evolved very distinct races at different levels in the continuous forest show a sudden change from one form to the other, as though the cumulative effect of the environment reached a threshold level, beyond which the change was sudden. The grassland races are isolated, so this criterion cannot be applied to them. The one species in which the races are

slightly differentiated (*Collocalia esculenta*) shows a gradual change with increased altitude.

In the forms with variations insufficient to recognize as races there is a gradual variation with altitude.

The exact levels to which the grassland races are restricted in part may be due only indirectly to climate acting on the vegetation. Temperature appears to be the single factor which changes most constantly in reference to altitude, and however the result is produced the larger size of the higher altitudinal populations appears correlated with the lower temperatures. This appears to be true only for minor variations, the most extreme of which form well-marked races.

Variation does not appear to be restricted to any one vertical level but may appear within almost any range of altitude, though in the present work it was not perceptible in less than 800 meters of altitude.

CONCLUSIONS

Lower temperature, caused by increased altitude, is in many species correlated with the increased size of the higher altitudinal representative of the same species or race of bird. The effect of varying humidity, caused by different conditions in the mountains, if such exist, cannot be evaluated.

When small differences exist between altitudinal representatives there tends to be gradual intergradation; when greater differences, as between well-marked races, are present, the change appears more abrupt, suggesting that here we have the forerunners of species. But species within a genus do not show such correlations. Usually there appears to be no correlation between the montane and lowland species of the same genus to suggest that the mountain species have evolved from the present lowland forms.

This suggests that the differences between altitudinally representative populations within a species, and that between altitudinally representative species, is more than one of degree only; that altitudinally representative species are not brought into being by only a continuation of the action of the forces which produced subspecies. Birds are restricted to certain levels on the mountain slopes, possibly through temperature, and this isolation allows species and genera to evolve independently at different altitudes. Climatic factors may perhaps speed up these changes, but the resultant variations are not as closely correlated with the lowered temperature as are the minor variations within species.